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HESLERODIDAE (CHONDRICHTHYES, ELASMOBRANCHII), A NEW FAMILY OF PALEOZOIC PHALACANTHOUS SHARKS

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ABSTRACT

A new family of extinct chondrichthyans (Heslerodidae) is created, containing the Paleozoic phalacanthous (fin-spine-bearing) shark *Heslerodus divergens* (known from fairly complete skeletal remains), plus two genera known only from isolated dorsal-fin spines, *Bythiacanthus* St. John and Worthen, 1875, and *Avonacanthus* gen. nov. Two species are retained in the genus *Bythiacanthus* (*B. vanhornei*, *B. siderius*), and *Glymmatacanthus* is synonymized with *Bythiacanthus*. *Avonacanthus* is probably a cladistically primitive member of the Heslerodidae.

Introduction

Many examples of isolated Paleozoic shark-fin spines have been described in the literature, but in most cases the kinds of sharks that possessed them are unknown. Bilaterally symmetrical spines are located at the dorsal midline in front of the dorsal fins in various extant sharks (e.g., *Squalus*, *Heterodontus*) and in some articulated fossil sharks (e.g., *Hybodus*; Maisey, 1978, 1979). In the past, many of these Paleozoic fossil spines were simply lumped together as an ill-defined assemblage of "ctenacanths," characterized by the presence of two dorsal-fin spines but supposedly lacking the apomorphic characters of hybodonts or neoselachians (Maisey, 1975). Collectively, "ctenacanths," hybodonts and neoselachians have been characterized as phalacanthous sharks (Zangerl, 1973) although it is unlikely that these are monophyletic when modern anacanthous (spineless) taxa are excluded. Furthermore, the phylogenetic relationships of Paleozoic phalacanths to their contemporary anacanthous relatives (e.g., symmoriids) or to Paleozoic sharks in which only a single dorsal spine is present (e.g., stethacanthids, xenacanths, some cladoselachians), are unresolved. The type species of *Ctenacanthus* (*C. major* Agassiz, 1837, p. 10) is still known only from isolated fin spines with ridges (costae) ornamented with fine pectinations (as are all the nominal species still referred to this genus; Maisey, 1981), although two Upper Devonian phalacanthous sharks from the Cleveland Shale (*C. compressus*; Dean, 1909; Maisey, 1981, 1984; "*Tamiobatis vetustus*" Williams, 1998) possess dorsal-fin spines very similar to those of *C. major*. As an additional complication, some Paleozoic sharks appear to have paired pectoral-fin spines with *Ctenacanthus*-like pectinate ornament (e.g., *Doliodus* and perhaps *Antarctilamna*), although it is still unclear whether such forms also possessed dorsal spines.

It would clearly help resolve this systematic and phylogenetic conundrum if different kinds of Paleozoic fin spines could be reliably associated with other skeletal remains. Among extant sharks, many aspects of fin-spine morphology (including shape, curvature, depth of insertion, internal structure, histology, ornament pattern, and presence or absence of posterior and posterolateral denticles) are often highly conserved, and it can be difficult (or impossible) to distinguish between the fin spines of certain modern genera. For example, the enameloid layer forming the mantle in fin spines of both *Squalus* and *Centroscymnus* is smooth and continuous, but in both *Etmopterus* and *Deania* it is restricted to three narrow costae (one anteriorly plus a pair posterolaterally), and in some forms there is no ornamented mantle whatsoever, for example in adult fin spines of extant *Oxynotus*, *Euprotomicrus*, and some Jurassic batoids (e.g., *Belemnobatis*, *Spathobatis*; Schweizer, 1964; Maisey, 1976, 1979). In Mesozoic hybodonts, fin-spine morphology is often highly conserved; those of *Hybodus*, *Egertonodus*, *Acrodus*, *Tribodus*, *Palaeobates*, and even the Pennsylvanian *Hamiltonichthys* are practically indistinguishable from each other. Exceptionally, an unusual fin-spine ornament pattern seems to characterize a single genus. For example, there is only a single narrow anterior costa in the extant neoselachian *Centrophorus*, and fin spines in the Mesozoic hybodont *Asteracanthus* are ornamented with longitudinal rows of large tubercles instead of continuous ribs (although intermediate morphologies blur even this distinction; e.g., *A. verrucosus*, representing a rare case of an ornament pattern which changes disto-proximally from ribs to tubercles; Egerton, 1854; Woodward, 1916).

Morphological and ontogenetic studies of modern shark-fin spines show that sclerogenetic tissues forming the spine mantle occur only at the base of the ornamented area, where they are deposited directly on the external surface of the underlying spine trunk, and investigation of fossil spines supports a similar developmental interpretation (Markert, 1896; Maisey, 1978, 1979). Elasmobranch fin-spine ornament therefore always seems to have been deposited sequentially and in a distal-proximal

direction. More importantly, the ornament in modern elasmobranch fin spines does not develop by secondary fusion of previously-formed mantle hard tissues, and does not involve the addition of secondary-mantle hard tissue between pre-existing ornament. Instead, the different ornament patterns (tubercles, costae, continuous mantle deposits) result from different (and fluctuating) rates and periodicities of mantle scleroblast activity, and do not involve the secondary deposition or re-working of mantle hard tissues. An identical mode of growth and enlargement can be postulated for fossil elasmobranch fin spines, where curved "growth lines" representing periodic pauses in scleroblastic activity are often observed passing across the ornamented mantle region and more or less parallel to the proximal margin of the ornament. Such indicators of periodic disto-proximal ornament accretion would be obliterated if there was secondary growth of mantle hard tissues between pre-existing areas. Even in spines with a tuberculate ornament, individual tubercles are frequently aligned in curved series running across the spine rather than longitudinally. Where tubercle formation is temporarily interrupted or suspended during spine growth, a space may form across the longitudinal tubercle rows (e.g., near the base of the ornament in the *Bythiacanthus* spine shown in Figure 1F–G). Thus, as in modern shark fin spines, mantle sclerogenesis in the fossils was (a) confined to the mantle base, (b) independent of proximal extension of the fin spine, and (c) coordinated across the entire ornament field throughout life irrespective of whether the ornament is broad, linear, or consists of individual tubercles.

One important systematic consequence of this morphological conservatism is that isolated fossil spines can often be assigned fairly reliably to already-established families or other supra-generic taxa, but rarely to genus or species. Although different fin-spine morphologies are certainly recognizable, the vast majority of extinct species founded on isolated fin spines probably do not represent equivalent or consistent operational taxonomic units (OTU's) and should not be considered valid without corroborative morphological data from other sources (e.g., teeth or skeletons).

This paper attempts to define a previously unrecognized higher taxon of extinct phalacanthous sharks that was first known only from isolated (but very distinctive) fin spines described under the generic name *Bythiacanthus* (St. John and Worthen, 1875, p. 445). The inspiration for this paper comes from Alexander Ivanov's and Michal Ginter's seminal work on phoebodontid and cladodont teeth, particularly the recognition (first noted by Ivanov during the mid-1990s; see Ginter, 2002, p. 554) that the teeth of the Pennsylvanian phalacanthous shark described by Williams (1985, p. 124) as *Phoebodus heslerorum* are identical to those described more than a century earlier under the name *Cladodus divergens* (Trautschold, 1879, p. 51). Ginter (2002) documented differences between the teeth of "*Phoebodus*" *heslerorum* and *Phoebodus* sensu stricto, and recommended that the former should not be referred to that genus (or even to the Family Phoebodontidae as defined by Williams, 1985, p. 124). Instead, Ginter (2002) erected a new genus (*Heslerodus*) and synonymized *P. heslerorum* with *H. divergens*. He retained *Phoebodus* in the Family Phoebodontidae, but removed *Heslerodus* as *incertae familiae*.

It has been noted elsewhere that the fin spines of this shark closely resemble those of *Bythiacanthus* (Maisey, 1982, p. 7). Recently, after examining specimens of *P. heslerorum* and *Bythiacanthus* in the Field Museum of Natural History (April 2004), I was able to confirm this similarity and concluded that these taxa are related. Furthermore, after examining the holotype of "*Oracanthus*" *lineatus* Newberry, 1897 (also in the Field Museum collection), I concluded that it is really an incomplete *Bythiacanthus* fin spine (a revision of *Oracanthus* is long overdue but is beyond the scope of this work).

On face value, this represents a simple taxonomic exercise; *Bythiacanthus* should take priority over *Heslerodus*, and the shark described by Williams (1985, p. 124) should be renamed *Bythiacanthus divergens*, sinking both the genus *Heslerodus* and the species *heslerorum*. Alternatively, we could go further and regard *Heslerodus divergens* as a synonym of *Bythiacanthus vanhornei*, thereby sinking all the names previously attached to William's (1985, p. 124) shark. Either conclusion might be justified if we were dealing with entire specimens of all the taxa involved and could compare spines, teeth, and other features. However, given the fragmentary nature of the critical type specimens, in this case all we would create is a chimeric taxon known from complete individuals but bearing the name of an isolated fin spine, while burying the somewhat more useful species name *divergens* (founded on isolated but distinctive teeth). In my opinion this is not progress but confusion, because we know nothing about the dentition and skeletal features in the type species of *Bythiacanthus* (*B. vanhornei* St. John and Worthen, 1875, p. 445). Consequently, there seems to be no empirical basis or practical justification for making *Heslerodus divergens* a synonym of *Bythiacanthus vanhornei*. On the other hand, Ginter's (2002) argument for synonymizing *heslerorum* with *divergens* is based on observed dental similarities, a reasonable proposal since most modern shark teeth are identifiable to genus if not species. Thus, the preferred course of action here is to retain *Heslerodus* and *Bythiacanthus* as distinct genera, with revised generic-level diagnoses, and to place both of them into a new Family Heslerodidae. In addition, some nominal species previously referred to *Bythiacanthus* (Maisey, 1982) are removed here to a new genus, which is also referred to the Heslerodidae. By taking this course, *Heslerodus* is retained as a valid taxon (a useful attribute in future phylogenetic analyses, because many aspects of its skeletal morphology are known) while recognizing its similarity to other Paleozoic taxa founded on less satisfactory, fragmentary material.

Systematic Paleontology

Class Chondrichthyes Huxley, 1880
Subclass Elasmobranchii Bonaparte, 1838
Family Heslerodidae new family

Diagnosis

Extinct elasmobranchs possessing two dorsal-fin spines with a stout rhomboidal profile, often though not invariably compressed laterally, posterior wall convex apically (sometimes exaggerated by diagenetic compression of fossil) and extremely short (level of posterior closure 75–95 percent of spine height), spine mantle consists of longitudinal rows of large rounded tubercles bearing radial striations (frequently abraded apically), tubercle rows increase proximally by primary bifurcation anteriorly and by insertion between other rows marginally, spines lack retrorse posterior and/or posterolateral denticle rows.

Included genera

Heslerodus Ginter, 2002; *Bythiacanthus* St. John and Worthen, 1875; *Glymmatacanthus* St. John and Worthen, 1875; *Avonacanthus* new genus.

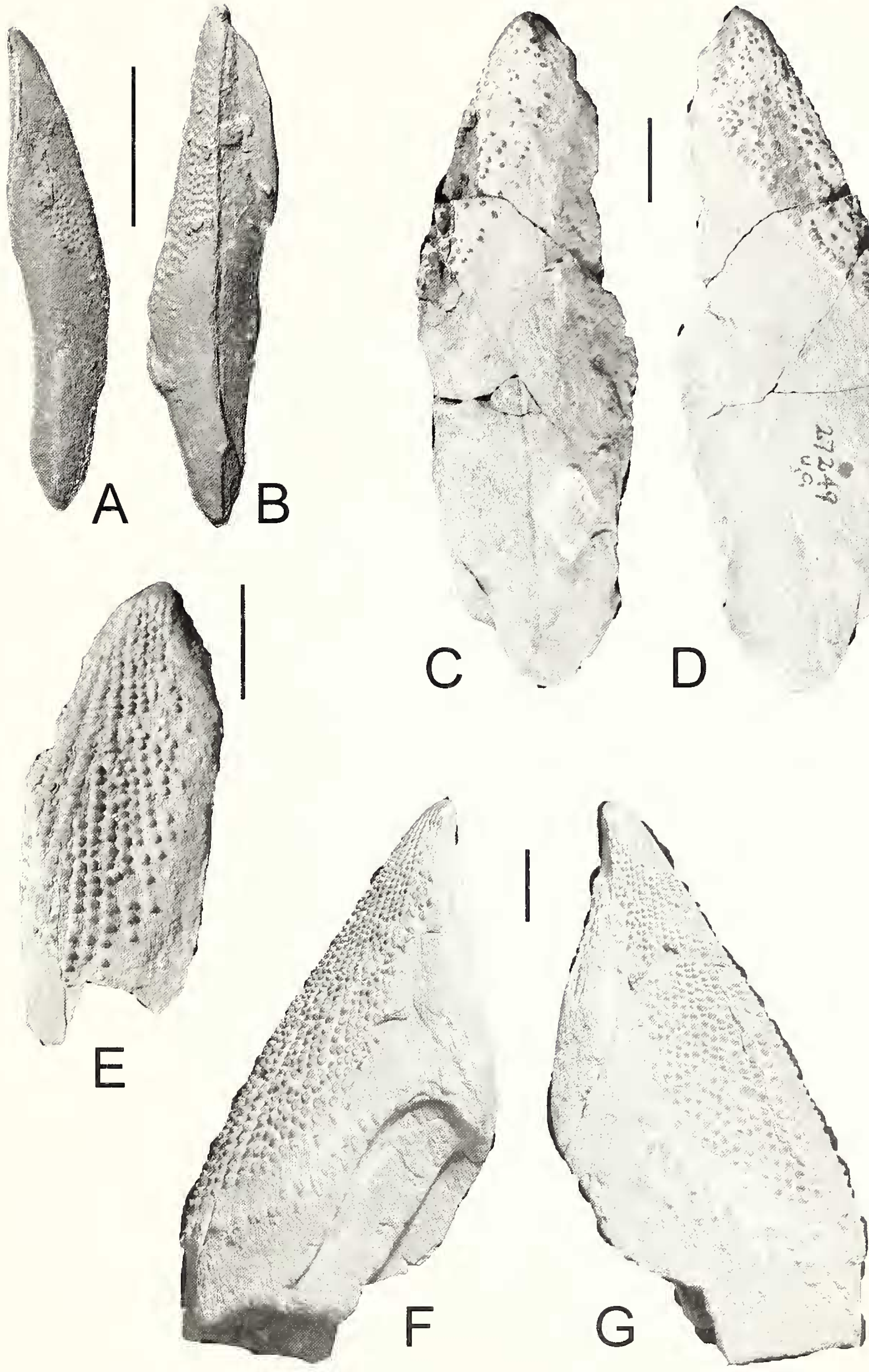


Figure 1. A–B, *Heslerodus divergens* (Trautschold), Middle Pennsylvanian, Parke County, Indiana. A, FMNH PF 8171, complete isolated anterior dorsal-fin spine, Mecca Quarry, right lateral view. B, FMNH PF2473, complete isolated anterior dorsal-fin spine, Logan Quarry, left lateral view. C–D, *Bythiacanthus vanhornei* St John and Worthen, genoholotype FMNH UC 27249, Middle Mississippian, Meramec Group, Upper St. Louis Limestone, Alton, Madison Co., Illinois, complete but inadequately prepared dorsal-fin spine in left and right lateral views. E, fragmentary holotype (only the apical region is preserved) of *Oracanthus lineatus* Newberry, synonymized here with *Bythiacanthus siderius* (Leidy, 1873), FMNH UC 9918, Meramac Group, St. Louis Limestone, Washington County, Indiana, left lateral view. F–G, *Bythiacanthus vanhornei*, lateral views of dorsal-fin spine lacking a small part of its base, previously misidentified as *Oracanthus* sp., FMNH UC 2197, Mississippian, Hardin County, Kentucky; note the gap in tubercles near the base of the ornamented region, indicating a pause in tubercle formation late in spine development. All scale bars equal 20 mm.

Comments

Collectively, the high level of posterior closure, massive unornamented spine trunk, and prominent anterior saddle suggest that heslerodid fin spines were deeply inserted in the body of the shark, and that most were probably inclined strongly backwards. As with all fossil fin spines, the shape of the posterior spine wall is commonly distorted by post-mortem deformation, because isolated spines are frequently subject to lateral compression after burial, causing the posterior wall (which is usually thinner than the adjacent lateral and anterior walls) to buckle outward. A spine with an originally flat or weakly convex posterior wall may therefore appear to have pronounced convexity following taphonomic and diagenetic distortion (involving localized plastic and/or brittle failure of spine hard tissues), although this can usually be detected by careful inspection.

Genus *Heslerodus* Ginter, 2002

Emended diagnosis

Heslerodid with fin spines strongly flattened laterally, tubercles slightly elongated and usually not contacting each other, distributed erratically on spine surface and exposing the outer vascularized surface of the underlying spine trunk, ornament extending over half the fin-spine height, level of posterior closure 70–75 percent of spine height; teeth with crown composed of three long, recurved main cusps, and usually two intermediate, smaller cusplets. Median cusp slightly larger than or equal to lateral main cusps in size, lateral cusps sigmoidal, strongly divergent mesiodistally (around 80–90°), tooth base rounded, with a distinct labial concavity and a lingual torus usually with two buttons on its apical surface.

Type species

Heslerodus divergens (Trautschold, 1879, p. 51).

Comments

Ginter and Ivanov (1992) noted that teeth in the phalacanthous shark named *Phoebodus heslerorum* by Williams (1985, p. 124) differ from those in the type species *P. sophiae* St. John and Worthen (1875), in which the median cusp is always slightly shorter than the lateral main cusps and the tooth base bears only a single median button on its apical surface. Ginter (2002) subsequently placed "*P.*" *heslerorum* in a new genus *Heslerodus*, and also recognized that its teeth are identical with those named *Cladodus divergens* by Trautschold (1879), which Ginter considered are distinct from *Cladodus* sensu stricto. However, Ginter's (2002) diagnosis of *Heslerodus* was limited to dental characters, whereas in the present work the diagnosis is expanded to include additional features involving fin spines (it could also include features of the endoskeleton, but that is beyond the scope of this work). The concave labial margin of *Heslerodus* teeth is an especially important feature that has not been observed in teeth referred to *Phoebodus* (M. Ginter, personal communication, 2004). Williams (1985, p. 124–131, plates 16–17) illustrated several fin spines of *H. divergens*, and two specimens are illustrated here (Figure 1A–B).

Heslerodus divergens (Trautschold, 1879)
Figure 1A–C

Cladodus divergens Trautschold, 1879, p. 51, Pl. 6, no. 11.
Phoebodus sp. Case, 1973, fig. 47.
Phoebodus n. sp. Zangerl, 1981, figs. 56–58.
"*Cladodus*" sp. Schultze, 1985, fig. 3.5.
Phoebodus heslerorum sp. n. Williams, 1985, p. 124–131, figs. 22–23, Pl. 16–17.
"*Cladodus*" *divergens* Trautschold Ivanov, 1999, p. 276–277, fig. 3, Pl. 7.1.
Heslerodus divergens (Trautschold) Ginter, 2002, p. 548–551, fig. 1A–C, 2.

Diagnosis

As for genus.

Holotype

Institute of Zoology, Wroclaw University, Wroclaw, Poland, Pch/617, the largest and most complete of three teeth catalogued under this number (Ginter, 2002), described and figured by Trautschold (1879, p. 51, Pl. 6, no. 11).

Comments

The holotype of *Phoebodus heslerorum* Williams, 1985 is reposited in the Field Museum of Natural History (PF 8170, Pennsylvanian, Westphalian Upper C, Des Moines Series, Linton Fm., Liverpool Cyclothem, Mecca Quarry Shale, Parke County, Indiana). It consists of a disarticulated skull, a partial pectoral fin, and both dorsal-fin spines. *Heslerodus divergens* is the only heslerodid known from skeletal remains. According to Ginter (2002), *Heslerodus divergens* teeth have a stratigraphie range from the Late Carboniferous (Bashkirian–Gzhelian) probably through the Lower Permian (Asselian). The species is recorded from Russia (Upper Carboniferous of the Moseow region and the Pechora Sea region of Arctic Russia) and North America (Pennsylvanian of Indiana, Nebraska, Ohio, Pennsylvania, and Wyoming; Lower Permian of Kansas). No teeth referable to *Heslerodus* are known from the Lower Carboniferous. Thus, if the Lower Carboniferous taxa discussed below are correctly referred to the Family Heslerodidae, their teeth were probably different from those of *Heslerodus*.

Bythiacanthus St. John and Worthen, 1875
(= *Glymmatacanthus* St. John and Worthen, 1875)

Emended diagnosis

Heslerodid with fin spines strongly compressed laterally, producing a very deep cross-section so that the anteroposterior dimension is 3 to 4 times the spine width; spine ornamented with large round tubercles with radial striations (often lost by abrasion), tubercle bases sometimes separate and sometimes distributed erratically but more commonly united, especially in longitudinal rows, revealing little of the underlying trunk surface; very high level of posterior closure (85–95 percent of spine length).

Type species

Bythiacanthus vanhornei St. John and Worthen, 1875, p. 445.

Comments

Maisey (1982) referred several nominal species founded on isolated fin spines to the genus *Bythiacanthus* in addition to the type species. However, some of those fin spines differ from the type species in not being strongly compressed laterally and are removed here to another genus (see below).

Bythiacanthus vanhornei St. John and Worthen, 1875
Figures 1D, 1F–G, 2A

Bythiacanthus vanhornei St. John and Worthen, 1875, p. 445, Pl. 17, no. 1; Maisey, 1982, p. 3, fig. 1A–I.

Diagnosis

Bythiacanthus with fin spines ornamented with sparse, scattered tubercles arranged in disorganized fashion, and confined to the apicalmost part of the spine.

Holotype

Field Museum of Natural History UC 27249, Middle Mississippian, Meramec Group, Upper St. Louis Limestone, Alton, Madison Co., Illinois. Complete fin spine, approximately 16.5 cm total length.

Comments

While it is possible that the type specimen of *Bythiacanthus vanhornei* represents an abnormally developed fin spine in which the regular deposition of tubercles had become disrupted, it is retained here as a distinct species. It is not uncommon for fossil fin spines to display irregularities in their ornament (e.g., in hybodonts; Maisey, 1978), but this is usually quite local in extent. Comparison of St. John and Worthen's (1875) original figure with the photographs here show that although the specimen is sparsely ornamented, matrix still covers much of its surface and may obscure smaller tubercles (cf. Figure 1C–D).

Bythiacanthus siderius (Leidy, 1873)
Figures 1E, 2B–J

Asteracanthus siderius Leidy, 1873, p. 313, Pl. 32, no. 59.
Glymmatacanthus irishi St. John and Worthen, 1875, p. 447, Pl. 17, no. 2.
Oracanthus lineatus Newberry, 1897, p. 289, Pl. 22, fig. 5.
Ctenacanthus solidus Eastman, 1902, p. 313; Eastman, 1903, Pl. 7, no. 3.
Ctenacanthus ianishevskyi Khabakov, 1928, p. 23, Pl. 3, nos. 5–10.
Bythiacanthus ianishevskyi (Khabakov) Maisey, 1982, p. 5, figs. 2G–K.
Bythiacanthus solidus (Eastman) Maisey, 1982, p. 5, figs. 3A–B.
Bythiacanthus siderius (Leidy) Maisey, 1982, p. 6, figs. 1J–L.

Diagnosis

Bythiacanthus with fin spines ornamented with numerous large tubercle rows commonly arising at or near anterior midline and passing obliquely across spine upper lateral surface, sometimes also arising by bifurcation farther laterally, posterior rows considerably shorter and more recurved than those farther anteriorly, forming a very oblique level of insertion.

Holotype

The whereabouts of the holotype is presently unknown. According to Leidy (1873, p. 313) the specimen was reputed to be from the "Sub-Carboniferous" of Glasgow, Tennessee. If that age is correct, this is by far the earliest known *Bythiacanthus*. However, its age has clearly always been problematic and could be Mississippian.

Comments

It is not an entirely satisfactory situation that the holotype was not available at the time of this revision, since several nominal species are synonymized here with *Bythiacanthus siderius*. It is nevertheless clear from the original description and figure that the holotype should not be referred to *Asteracanthus* (Maisey, 1982). St. John and Worthen (1875, p. 477) suggested that Leidy's (1873, p. 313) species *siderius* may be conspecific with *Bythiacanthus vanhornei*. However, the tubercles in Leidy's very fragmentary type specimen are better organized into vertical rows than in the holotype of *B. vanhornei*. Orderly tubercle rows are also present in AMNH 1826, a fairly complete fin spine referred to *Bythiacanthus siderius* by Maisey (1982, Figure 1J–K).

Two additional examples of *Bythiacanthus* fin spines are reposited in the Field Museum collection. One of them is the holotype of *Oracanthus lineatus* Newberry, 1897 (FMNH UC 9918; Figure 1E), from the Meramac Group, St. Louis Limestone of Washington County, Indiana. The other example is a very large fin spine previously misidentified as *Oracanthus* sp. (FMNH UC 2197; Figure 1F–G), from the Mississippian of Hardin County, Kentucky. The ornament and shape of these two spines is completely different from the type species of *Oracanthus* (*O. milleri*; Agassiz, 1837, p. 13), and they do not pertain to that genus. However, FMNH UC 9918 is very close in size, shape and ornament to AMNH 1826, and it is concluded that *Oracanthus lineatus* is synonymous with *B. siderius*.

Glymmatacanthus irishii (the type species of the genus) is also considered synonymous with *Bythiacanthus siderius* (*Glymmatacanthus* was already regarded as a junior subjective synonym of *Bythiacanthus*; Maisey, 1982). Other species referred to *Glymmatacanthus* (e.g., *G. rudis*, *G. petrodoides*; St. John and Worthen, 1875) could also pertain to *Bythiacanthus*, but are founded on specimens that are too fragmentary to present any diagnosable features.

Eastman's (1903) *Ctenacanthus solidus* and Khabakov's (1928) *Ctenacanthus ianishevskyi* were both referred to *Bythiacanthus* by Maisey (1982), but were retained as separate species. However, in the absence of any unique features, there seems little reason to continue separating them from *B. siderius*, and they are here placed into synonymy with that species. Two species formerly included in *Ctenacanthus* (*C. peregrinus*; Khabakov, 1928; *C. lucasi*; Eastman, 1902) were reassigned by Maisey (1982) to *Bythiacanthus*, but are now removed to a new genus (see below).

Fin spines referred here to *Bythiacanthus siderius* can be categorized into two distinct forms, distinguishable by their shape and profile. One form has a strongly rhombic profile and a massive anterior saddle, below which the leading edge of the trunk slopes at an angle of almost 80° away from the leading edge of the ornamented mantle region. Examples of this form include the specimens referred to *B. ianishevskyi* by Khabakov (1928) and Maisey (1982), as well as the paratype of *B. solidus* (Eastman, 1903, Pl. 7, no. 3: also see Maisey, 1982, fig. 3B). The other form is less rhombic and has a much smaller anterior saddle, below which the trunk slopes less abruptly away from the leading edge of the ornamented region (ca. 170°). Examples of this form include AMNH 1826 and FMNH UC 2197 (Figure 1F–G). The holotype of *B. solidus* may also represent this form, although its saddle is not preserved (see Maisey, 1982, fig. 2A). Unfortunately, the type specimens of *Bythiacanthus siderius*, *Glymmatacanthus irishii*, and "*Oracanthus*" *lineatus* are not sufficiently complete to determine their original outline or the extent of the saddle.

It is possible that these two forms represent different taxa, but this is considered unlikely because in *H. divergens* the posterior fin spine is more rhombic in profile and has a more extensive saddle than the anterior one (e.g., FMNH PF 8170; Williams, 1985, Pl.

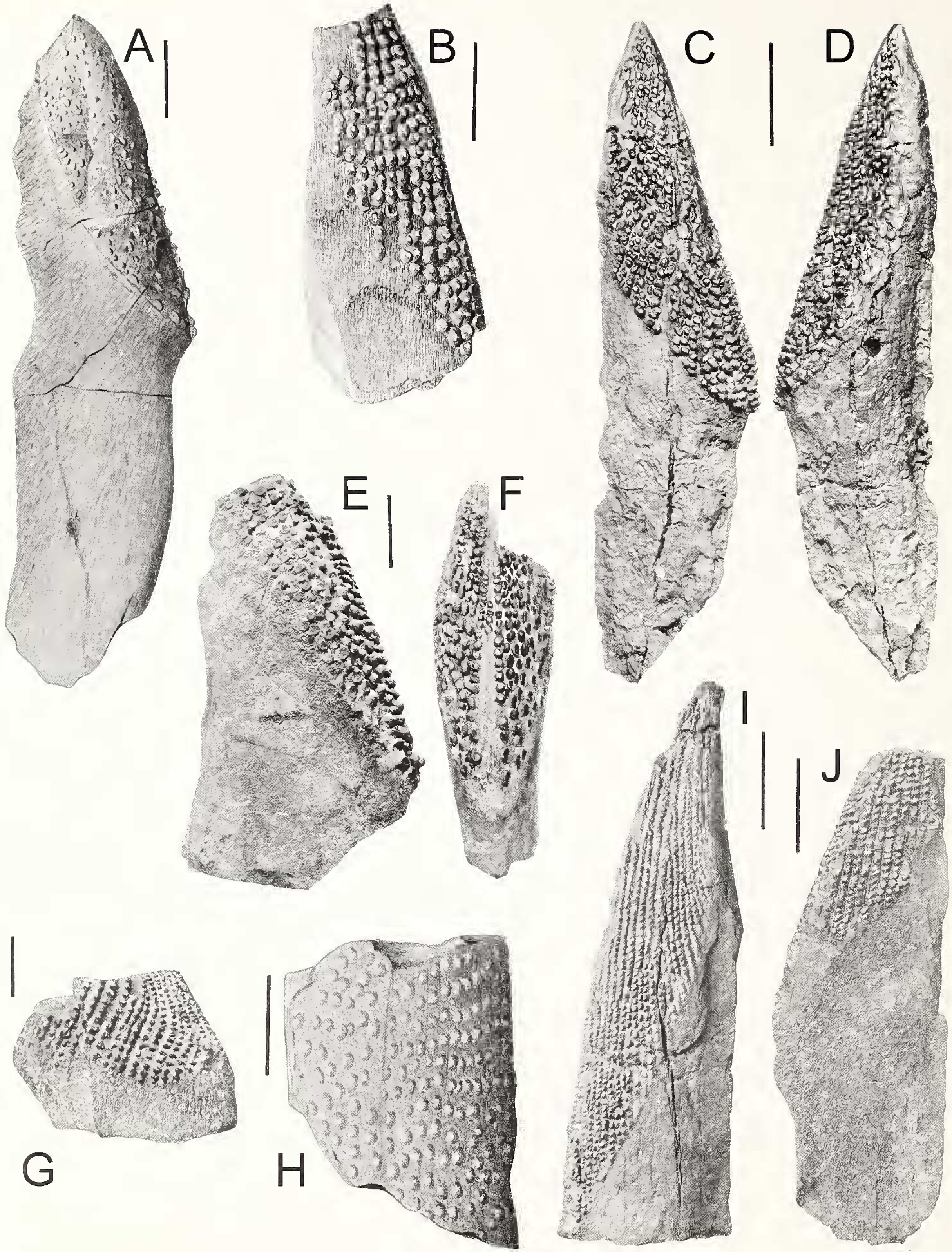


Figure 2. A, *Bythiacanthus vanhornei* St. John and Worthen; genoholotype FMNH UC 27249, complete dorsal-fin spine in right lateral view (from St. John and Worthen 1875, Pl. 17, no. 1). B, *B. siderius* (Leidy); holotype PAN S22:13 7835, dorsal-fin spine lacking apical and basal regions, right lateral view (from Leidy, 1873, Pl. 32, no. 59). C–D, *Bythiacanthus siderius* (Leidy), AMNH 1826, St. Louis Limestone, Alton, Illinois, right and left lateral views of complete dorsal-fin spine (from Maisey, 1982, Figure 1J–K). E–F, *Bythiacanthus siderius* (Leidy), AMNH 9594, dorsal-fin spine lacking apical region and part of base, right lateral and anterior views (from Maisey, 1982, fig. 1M, N). G, fragmentary holotype of *Ctenacanthus ianishevskyi* Khabakob (synonymized here with

16, figs. 5–6), although the difference is not as great as in the spines referred to *B. siderius*. Corresponding differences in anterior and posterior fin-spine morphology are also found in articulated skeletons of *Hybodus hauffianus*, where the posterior dorsal-fin spine has a well-developed saddle and is more erect, while the anterior spine has a relatively inconspicuous saddle and is inserted more obliquely (Maisey, 1978, p. 664). Collectively, these observations suggest that more rhombic *Bythiacanthus* fin spines are from the posterior dorsal fin while the less rhombic ones are from the anterior fin, and that their insertion angles relative to the main body axis were profoundly different. These shape differences are therefore not considered taxonomically significant.

HESLERODIDAE?
AVONACANTHUS new genus

Diagnosis

Heslerodid? with fin spines not strongly compressed laterally, C-shaped cross section widening below the ornament base; moderately high level of posterior closure; ornament with numerous closely-spaced and well-defined longitudinal rows of large tubercles extending more than half length of fin spine.

Type species

Ctenacanthus brevis Agassiz, 1837, p. 11.

Comments

The fin spines included here are distinguished from those referred to *Heslerodus* or *Bythiacanthus* in being more rounded in cross section and less rhombic in profile (Figure 3). However, they have a high level of posterior closure and are ornamented with large tubercles, as in *Heslerodus* and *Bythiacanthus*. *Avonacanthus* fin spines therefore share some but not all the specialized features of those genera. If *Avonacanthus* is a heslerodid, it may represent a cladistically primitive member of the group, since its fin spines are comparatively generalized except for the features just noted.

AVONACANTHUS BREVIS (Agassiz, 1837)
Figure 3A–G

Ctenacanthus brevis AGASSIZ, 1837, p. 11, Pl. 2, no. 2; DAVIS, 1883, p. 337, Pl. 43, fig. 3.
Ctenacanthus lucasi EASTMAN, 1902, p. 80, Pl. 6, no. 3.
Ctenacanthus peregrinus KHABAKOV, 1928, p. 25, Pl. 3, nos. 1–4.
Bythiacanthus brevis (Agassiz) MAISEY, 1982, p. 5, fig. 2A–F.
Bythiacanthus lucasi (Eastman) MAISEY, 1982, p. 5, fig. 3G.
Bythiacanthus peregrinus (Khabakov) MAISEY, 1982, p. 5, figs. 3C–F.

Holotype

Bristol City Museum and Art Gallery C 4154, Lower Carboniferous, Carboniferous Limestone, Avon Gorge, near Bristol, England. Isolated fin spine lacking the proximal part of the inserted region (Figure 3A–C).

Comments

The original figure of the holotype in Agassiz (1837, Pl. 2, no. 2) was not drawn from the specimen but was based instead on an earlier drawing made by William Buckland (see Figure 3A). Subsequent photographs of the specimen (Figure 3B–C) suggest that it was more complete in Buckland's time (the Bristol City Museum's paleontological collections were extensively damaged during the Second World War). Other fin spines resembling those of *Avonacanthus brevis* include the holotypes of *Ctenacanthus lucasi* Eastman, 1902, and *C. peregrinus* Khabakob, 1928 (Figure 3D–H). These species were referred to *Bythiacanthus* by Maisey (1982) and are regarded here as synonymous with *A. brevis*, based on general similarities in spine transverse sections and ornament pattern.

Discussion

The systematic arrangement adopted here is admittedly a compromise solution to an all-too-common problem in paleontology, namely how to maintain the individuality of a recently-described taxon known from fairly complete fossil remains, and to propose a higher-level relationship with other previously-named taxa known only from similar but extremely fragmentary fossils, even though the latter probably represent essentially undiagnosable species (and possibly genera). In fact, the present case is comparatively straightforward because the fin spines involved are highly distinctive, increasing the probability that they represent a monophyletic group of phalacanthous sharks. The fortuitous discovery of complete *Heslerodus* fossils (Williams, 1985) shows that teeth previously referred to *Cladodus divergens* are from a phalacanthous shark whose fin spines closely resemble those of *Bythiacanthus* in their distinctive shape and ornament.

The diagnostic features distinguishing *Heslerodus* and *Bythiacanthus* are admittedly subjective, because they are limited to features of the fin spines such as differences in the density, shape, and spacing of tubercles, the level of posterior closure, and the degree to which the spine profile approaches a rhombic shape. The absence of *divergens* teeth in the Lower Carboniferous provides additional biostratigraphic support for continued separation of *Heslerodus* and *Bythiacanthus*. The systematic importance of the slightly different tubercle arrangements noted in *B. vanhornei* and *B. siderius* is unclear; both taxa are retained as separate species here, but given the lack of systematically informative characters they could represent different genera, or variants of a single species (in which case *B. vanhornei* would become a junior subjective synonym of *B. siderius*).

Acknowledgments

I miss the discussions about early sharks I had with Mike Williams, and I regret he is not here to enjoy the ongoing

←

Bythiacanthus siderius), CNIGR 2421/2, Leningrad; Carboniferous Limestone C, Kuznetsk Basin, Siberia, right lateral view of dorsal-fin spine lacking apical and basal regions (from Khabakob, 1928, Pl. 3, no. 5). H, fragmentary holotype of *Glymmatacanthus irishii* St. John and Worthen (synonymized here with *Bythiacanthus siderius*), USNM 13537, Kinderhook Formation, Marshall Co., Iowa (from St. John and Worthen, 1875, Pl. 17, no. 2a), from an undetermined part of the spine mid-region, right lateral view. I, holotype of *Ctenacanthus solidus* Eastman (synonymized here with *Bythiacanthus siderius*), USNM 3383, Kinderhook Formation, Iowa, dorsal-fin spine lacking basal region, left lateral view (from Maisey, 1982, fig. 3A). J, paratype of *Ctenacanthus solidus* Eastman, USNM 4843, Kinderhook Formation, Iowa, dorsal-fin spine lacking basal region, left lateral view (from Eastman, 1903, Pl. 7, no. 3). All scale bars equal 20 mm.

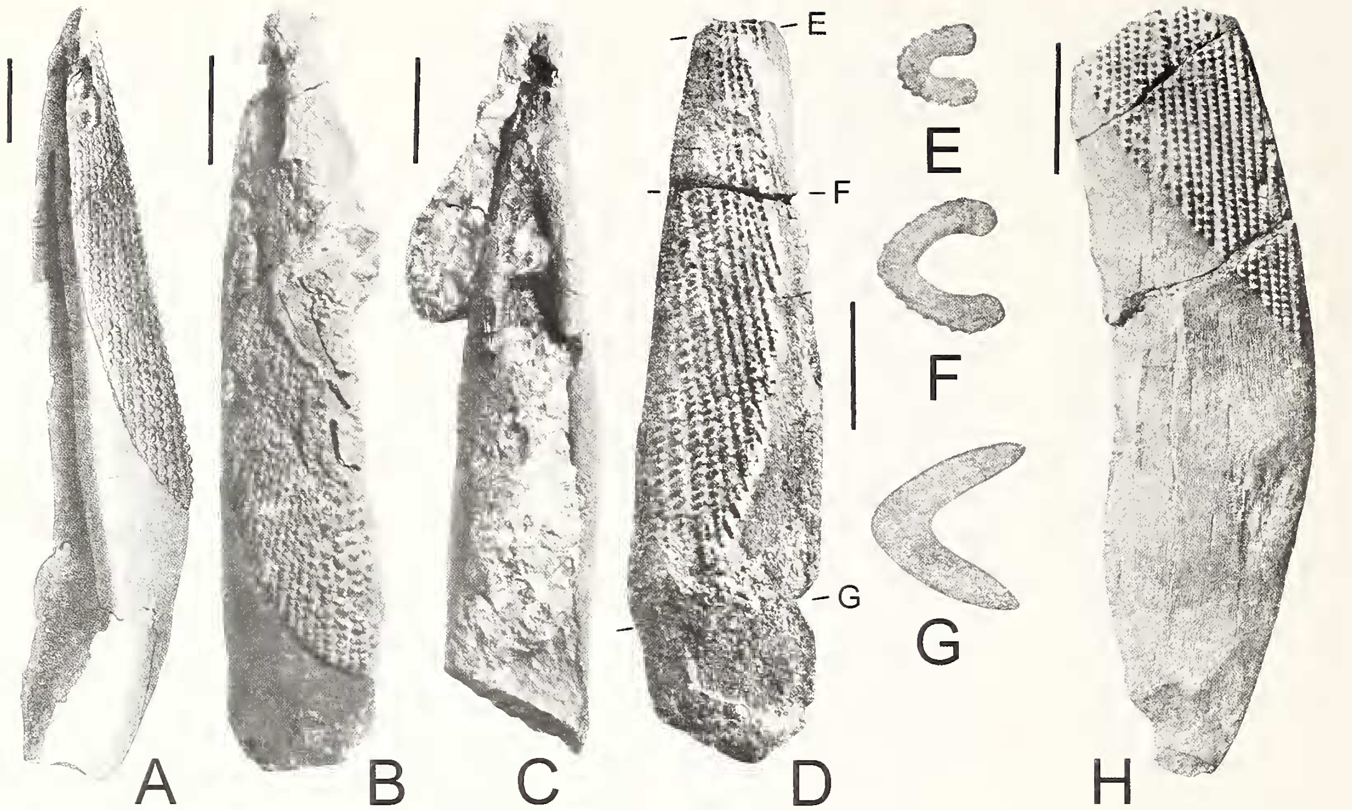


Figure 3. *Avonacanthus*, new genus. A–C, *Avonacanthus brevis* (Agassiz), genoholotype, C4154, Bristol City Museum and Art Gallery, U.K., Carboniferous Limestone (Avonian Z2 fish beds), Clifton, near Bristol. A, original figure (from Agassiz, 1837, Pl. 2, no. 2), right lateral view (slightly oblique) showing dorsal-fin spine with most of basal region. B–C, photographs of same specimen in lateral (B) and posterior (C) views, with less of the basal region preserved (from Maisey, 1982, fig. 2A–D; photos courtesy of BCMAG). D–G, *Ctenacanthus peregrinus* Khabakob (synonymized here with *Avonacanthus brevis*), holotype, CNIGR 2421/3, Leningrad, Carboniferous Limestone (Tournaisian C1), Roika Village, Tom River, Siberia, dorsal-fin spine lacking parts of apical and basal regions. D, right lateral view, E–G, transverse sections at levels indicated (from Khabakob, 1928, Pl. 3, nos. 1–4). H, *Ctenacanthus lucasi* Eastman (synonymized here with *Avonacanthus brevis*), holotype, USNM 4686, Kinderhook Formation, Iowa, dorsal-fin spine lacking much of its apical region, right lateral view (from Eastman, 1902, Pl. 6, no. 1). All scale bars equal 20 mm.

developments in our shared field of interest. Mike's untimely passing came just a few months before that of Bobb Schaeffer, so I have lost two good friends and colleagues in close succession. I am extremely grateful to M. Ginter for useful discussions about phoebodontid teeth and the distinctions between *Phoebodus* and *Heslerodus*. I thank him and an anonymous reviewer for providing many helpful comments and suggestions. I also thank L. Grande for permitting me to work in the fossil fish collection at the Field Museum of Natural History, the Bass Visiting Scientist Scholarship Committee for funding part of this investigation, and the support of the American Museum of Natural History in completing this work, and thank L. Meeker for creating additional illustrations for this paper at short notice.

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